

On the Swimming of *Dictyostelium* amoebae

The conventional mode for amoeboid locomotion is crawling. N. P. Barry and M. S. Bretscher recently demonstrated that *Dictyostelium* amoebae are also capable of swimming towards chemoattractants [1]. They hypothesized that the mechanism for swimming is intimately related to crawling. When crawling, the cell front bifurcates, and protrusions move backwards, relative to the cell. The authors conjecture that floating cells executing these same motions will swim. In this letter, we show that, indeed, the shape changes of a crawling cell are sufficient for swimming.

To obtain cell geometries, we flattened developed *D. discoideum* (cytosolic GFP in AX2) in an $\sim 4\mu\text{m}$ tall chamber [2]. Cells were imaged using confocal microscopy ($f_{\text{image}}=1/\text{s}$) for $500(\pm 140)$ s. From these images, cell contours were retrieved [3].

The contour curvature plot, 1A, shows that, indeed, protrusions move from the cell front towards the back. This behavior is also seen in the two-dimensional low Reynolds number swimmer of A. Shapere and F. Wilczek [4]. Therefore, crawling motion seems consistent with swimming.

To more rigorously evaluate this claim, we solved the Stokes flow with no-slip boundary conditions at the cell, and an open boundary, zero normal stress, a distance $250\mu\text{m}$ away. By calculating the appropriate counterflow (cf. [4]), we were able to determine the translational and rotational velocities for the cell, had the cell not been attached to a substrate.

We analyzed the virtual swimming velocity of $n = 13$ cells, and found that, for all cells, the time-averaged component along the direction of

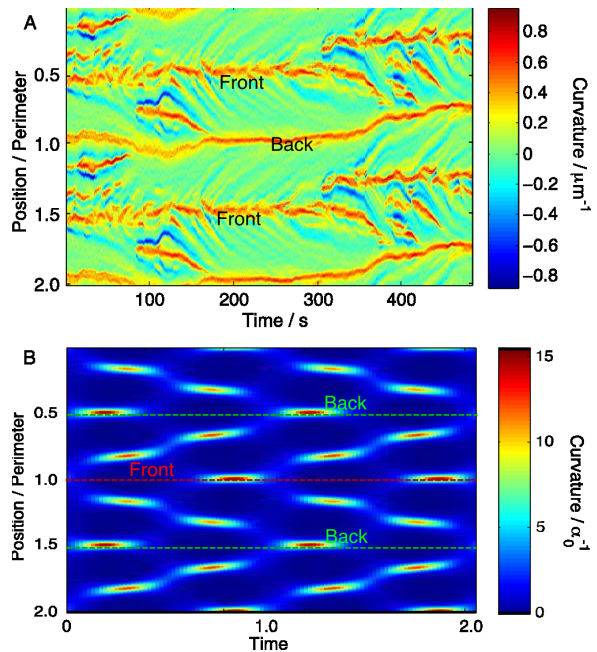


Figure 1: Curvature space-time plots for the contours of (A) a typical crawling cell and (B) the Shapere-Wilczek swimmer. To prevent a loss of detail at the edges, the curvature has been plotted over two contour lengths. Note the herringbone structure—regions of high curvature bifurcate at the front and travel towards the back.

polarization was positive.¹ The average directed swimming speed was $1.0(\pm 0.5)\mu\text{m}/\text{min}$. For crawling, this was found to be $12(\pm 7)\mu\text{m}/\text{min}$. The correlation coefficient $r = 0.6943$ with $p = 0.009$. Therefore, cells that crawl faster are also faster swimmers (figure 2).

Despite the qualitative agreement with [1], there are discrepancies. In [1], the cells swim at $4.2\mu\text{m}/\text{min}$ and crawl at $3.8\mu\text{m}/\text{min}$. Our

¹Defined as the direction from the cell's tail to its centroid.

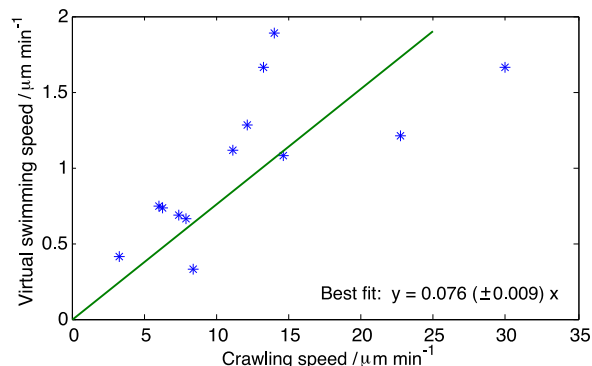


Figure 2: The crawling and virtual swimming velocities along the direction of polarization. Constrained least squares regression shows that the cells crawl 12 times faster than they swim.

crawling speed is 3 times higher, and our virtual swimming speed is 4 times lower. On the one hand, flattened cells are less active in producing pseudopodia (data not shown) and thus we expect the virtual swimmer to be slower. On the other hand, when confined between two plates, a cell may migrate more efficiently: a cell crawling without a ceiling is likely to produce a pseudopod away from the substrate, and only when this pseudopod contacts the substrate can produce propulsion. We expect the result to hold for neutrophils by analogy.

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References

- [1] N.P. Barry, M.S. Bretscher. (2010) *Dictyostelium* amoebae and neutrophils can swim. *PNAS* **107**:11376-80.
- [2] C. Westendorf, A.J. Bae, C. Erlenkamper, E. Galland, C. Franck, E. Bodenschatz and C. Beta. (2010) Live cell flattening. *PMC Biophysics* **3**:9.
- [3] É. Debreuve. Active Contour Toolbox, <http://www.i3s.unice.fr/~debreuve/code.php>
- [4] A. Shapere and F. Wilczek. (1989) Geometry of self-propulsion at low Reynolds number. *J. Fluid Mech.* **198**:557-85